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# Distribution and Status of the Mountain Gorilla (*Gorilla gorilla beringei*)—1959[1]

JOHN T. EMLEN, JR., & GEORGE B. SCHALLER
*Department of Zoology, University of Wisconsin, Madison, Wis.*

(Text-figures 1-5)

THIS report describes the results of a survey of the distribution of the Mountain or Eastern Gorilla (*Gorilla gorilla beringei*) as defined by Coolidge (1929) throughout the extent of its geographic range in the Kivu and Oriental Provinces of the Belgian Congo and the Kigezi District of Uganda. No attempt is made to review the literature or to summarize the data from museum specimens. The objective is to construct as complete a picture as possible of the distribution and status of these animals as of 1959. To this end historical records are included only as they shed light on the current situation.

The survey in its over-all objectives included comparisons of behavior and adaptations in various parts of the range and was organized as the first stage of a systematic study of the life history and ecology of the Mountain Gorilla. These latter aspects of the study are currently being pursued and will be reported at a later date.

The survey extended from early March to the end of July, 1959. Approximately four weeks were spent in the Birunga Volcano area, two in the Kayonza (Impenetrable) Forest of Uganda, two in the Lubero region west of Lake Edward, two in the Lake Kivu-Mt. Kahuzi country, two in the southern region bordering Lake Tanganyika and three in the broad equatorial forest west of the Rift Escarpment. Time did not permit a visit to the northern region which is largely inaccessible by road. Most of the survey work was done on foot in the first two regions and by car in the others.

[1]A supplement containing regional maps and tables summarizing the raw data and a list of authorities and references is available on request from the senior author.

The study was conducted under the sponsorship of the New York Zoological Society with funds partly from the Society and partly from a grant by the National Science Foundation. Full cooperation, including the provision of housing facilities and guides and the granting of permission to visit restricted areas, was tendered by the Institute of National Parks of the Belgian Congo. Helpful assistance was extended by the Institute for Scientific Research in Central Africa (I. R. S. A. C.) and the Uganda Game Department. Technical cooperation was offered by these organizations, by staff members of the Medical School of Makerere College, the Uganda Agricultural Research Station at Kawanda, the Virus Research Laboratory at Entebbe and the National Institute for Agronomic Research in the Congo (I. N. E. A. C.).

The list of persons whose assistance should be acknowledged is too long to be included in its entirety. A partial list is included as an appendix to this report.

## PROCEDURE AND METHODS

The data for this report are based, in the last analysis, on current observations in each area as recorded personally or as communicated directly to us by residents and visitors. The procedure followed may be considered as falling into three steps: (1) general reconnaissance of the whole region, (2) local reconnaissance and (3) on-the-spot checking of details.

The general reconnaissance was accomplished by examining reports and by interviewing government officials, prospectors, travelling missionaries and others. Published reports of early expeditions and surveys were also examined and a considerable correspondence was

established with experienced residents in all parts of the region. The information so assembled was useful in obtaining a preliminary picture of the outlines of distribution and a basis for intensive local work.

Local reconnaissance, the second step in the survey procedure, was accomplished largely through interviews with local administrators and regional native chiefs. European settlers were also visited as encountered or were deliberately sought out when reported to have pertinent experience or information. Their reports were often quite specific and detailed, but more often required further checking at the local level. Many of these people were able to call in natives from various parts of their regions to supplement, confirm or refute their reports.

Local checking of details was done personally on foot or by interviewing native residents. More than 400 local natives and native groups were interviewed. Workmen in the small road maintenance crews scattered every few kilometers along the Congo forest roads were generally well acquainted with conditions for several miles around their semi-permanent camps and proved to be one of our best sources of information. The elders of the small roadside villages also provided much helpful information. We usually stopped our car at a central point in a village and within a few minutes were surrounded by a few to 20 or more men eager to pool their knowledge of gorilla distribution and gorilla history in the immediate vicinity. Most of the reports were negative and these were, of course, as important as positive reports for charting the details of gorilla distribution. We repeatedly checked the accuracy of positive reports by challenging the informants to show us the evidence. Without exception they were able to do so.

Personal observations of gorillas and gorilla spoor were made whenever possible. In the Lubero and Uganda border regions personal observations provided the bulk of the data. In the other regions we personally checked at sample points and particularly where we had reason to question a reported occurrence. A foot transect was also used to cover a broad, roadless and relatively unknown area of equatorial forest in the western region. Except when we were led to known sites by locally experienced natives, the procedure was to follow trails as available into the heart of the area, then strike out in a straight line with a compass, looking for all beds, droppings, trails and other traces of gorilla activity and obtaining a crude quantitative index of the incidence of such traces per hour or mile of transect.

Data were recorded on the best large-scale maps available for each region (1:50,000, 1:200,000 or 1:500,000) and subsequently transcribed to a standard base (1:500,000, C. N. Ki, 1958) from which the distribution maps (Text-figs. 1 and 3) accompanying this report were prepared. A sample larger scale map is presented in Text-fig. 2.

## Geographical Distribution

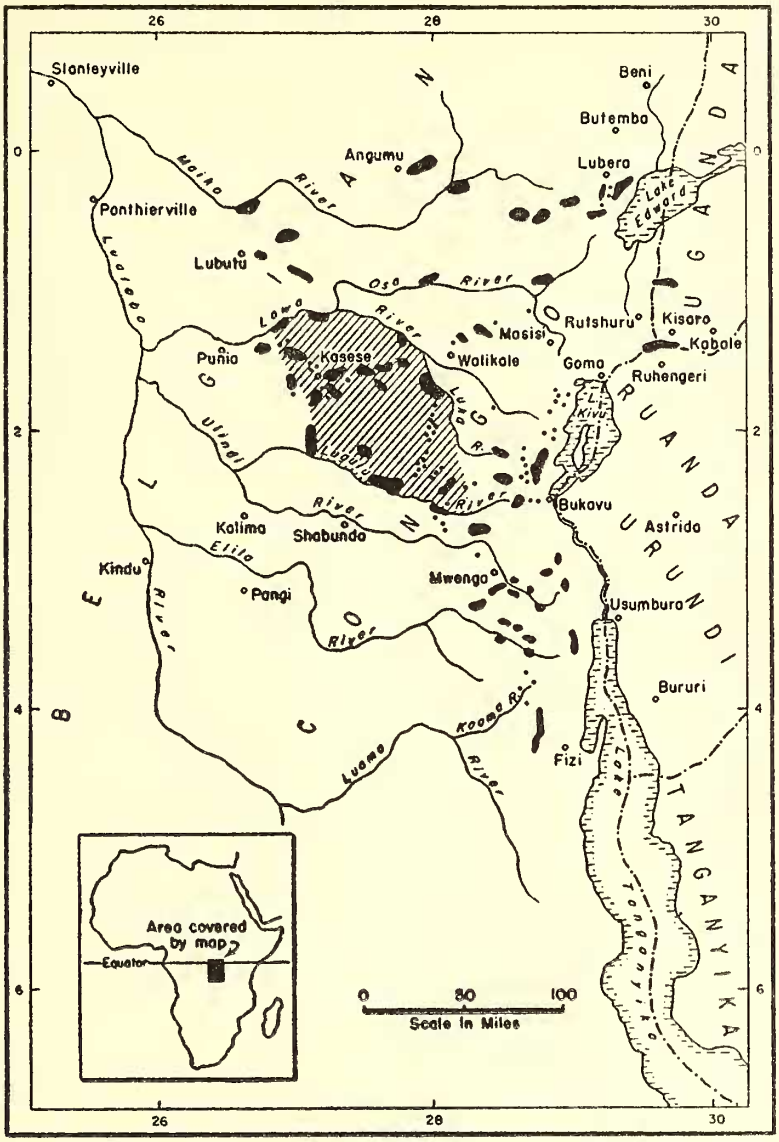
The range of the Mountain Gorilla extends from the equator south to about 4° 20′ south latitude, a distance of about 300 miles, and from longitude 26° 30′ east to the west escarpment of the Rift Valley at about 29° east longitude, with a small extension into mountain forests of the Valley floor north of Lake Kivu, an east-west distance of slightly more than 200 miles (Text-fig. 1). It is in the form of a triangle with its points near Lubutu on the northwest, Lubero on the northeast and Fizi on the south and covers an area of about 35,000 square miles. The boundaries are quite distinct along the east and southwest fronts, and no records of stragglers were encountered beyond these limits in fairly intensive surveys. We unfortunately have very little detailed information on the north boundary, however, and there may well be additional pockets in the Maiko Valley and westward toward Ponthierville.

Within the borders of this range, most of the gorillas are concentrated in about 60 more or less isolated tracts of 10 to 120 square miles each (solid black areas in Text-fig. 1), separated from each other by distances of 2 to 30 miles. Thus the area occupied by substantial populations is only about 1,900 square miles, or 5½ per cent. of the total area of the range.

A block of about 6,500 square miles in the western region between the Lowa and the Lugula Rivers (hatched areas in Text-fig. 1) apparently contains a relatively sparse but uniform population of wandering troops and individuals. The vast stretches of forest between and around these populated areas are essentially unoccupied except for stragglers—single adult or sub-adult males or occasionally small groups which leave the troops to live solitary lives as much as 20 miles from the nearest colony. Such animals are encountered at irregular intervals and in a variety of situations, sometimes establishing themselves for considerable periods of time near farms or native villages.

## Numerical Status

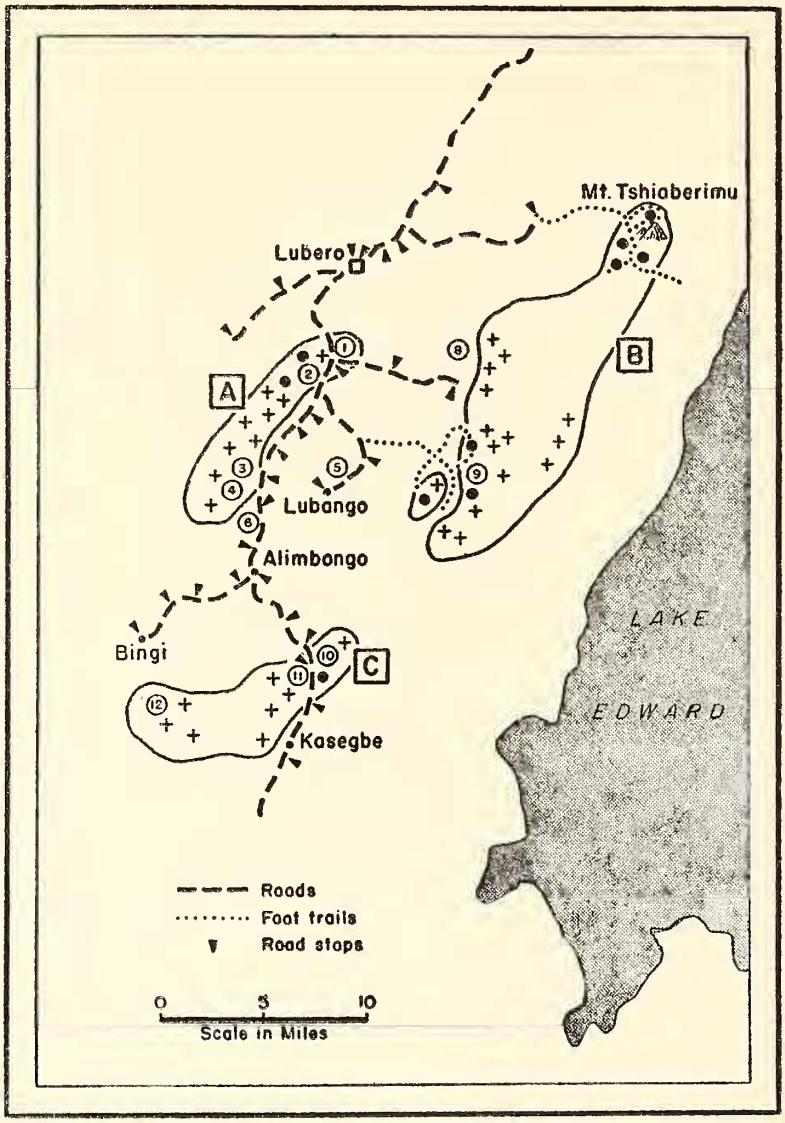
Although we have very inadequate data for estimating the numbers of gorillas present within the range described above, there is a legitimate




TEXT-FIG. 1. Geographic distribution of the Mountain Gorilla—1959. The sixty black areas indicate the location and approximate shape of sixty "gorilla areas" ranging in size from about 10 to about 100 square miles each. The small dots indicate records of stragglers outside of these areas. The hatching marks a central region of fairly continuous but sparse population. (Detailed maps and tables presenting a summary of the raw data on which the map is constructed may be had from the senior author on request. A sample map of this type is presented in Text-fig. 2).

demand for quantitative information on this rare and localized animal which should not be disregarded. We therefore submit the following data with the warning that the conclusions are extremely tenuous.

Intensive surveys of local gorilla populations were conducted on five plots in three areas in the northeastern part of the range. It was hoped that these surveys would provide indications of population densities in these areas. We found, however, that, because of the wandering habits of the gorilla, a survey conducted on a plot of 5 to 10 square miles over a period of a few weeks may be quite atypical of even the local situation. On one 10-square-mile plot, for instance, the population was known to have nearly quadru-




TEXT-FIG. 2. Details of the geographic distribution of the Mountain Gorilla in the Lubero Region (a sample of the regional maps from which the general map in Text-fig. 1 is constructed). Encircled numbers indicate the locations of specific records reported to us; large circular spots indicate the location of personal observations of gorillas or gorilla spoor; plus signs show where gorillas were reported to be present but without specific observations recorded. Dashed lines indicate routes travelled by car; dotted lines are those traversed on foot. Short bars at the side of the routes mark the places where local natives were interviewed.

pled through immigration shortly after our twenty-day survey was completed; on another, six days of intensive work over four of the six square miles revealed no fresh sign; then two troops were discovered together at the western end of the plot. Taking all factors into consideration we estimate that population densities in these areas generally averaged somewhere between one and five animals per square mile. Higher levels were encountered, but these were thought to represent temporary concentrations.

Calculations based on predation statistics provided another independent source of information on population size in the Lubero region where gorillas, coming close to villages or raiding native gardens, are commonly hunted with

spears. Data from the three hospitals serving this region showed an average of five cases of gorilla injury treated per year, all apparently the victims of counter-attacking gorillas. Hospital attendants and others estimated that this indicated an actual incidence of at least 10 injuries (half not reporting for treatment) per year. They and two patients who had sustained leg injuries also agreed that the number of raids organized against gorillas each year was considerably greater than the number of injuries, and that most of these raids were pressed until the offending gorilla was killed. Animals which inflicted injury, in particular, were marked for further raids of attrition and rarely escaped with their lives. Although these calculations are very crude, the figures suggest a slaughter of at least 20 and perhaps more than twice that number of gorillas in this 110-square-mile area every year. The large number of fairly fresh gorilla skulls (14) which we saw in the villages is further evidence of such a slaughter. While we still know very little about the population dynamics of these slow-reproducing animals, the population level required for survival and maintenance under this type of predation pressure must be of the same order of magnitude as that indicated in the plot surveys.

Comparisons of population level in different parts of the range were essayed by indices based on the number of bed sites, droppings or feeding areas encountered per mile or per hour of trailless foot transect. Unfortunately conditions of vegetation varied so greatly that direct comparisons of figures are of little value. For instance, beds were more easily seen in bamboo forests where the animals generally built 8 to 10 feet off the ground than they were in the broad-leaf forest where most of them bedded on the surface. Tallies of droppings were also difficult to equate because of marked differences in the density of concealing ground cover. Thus, the relative abundance of gorillas in different parts of the range could only be crudely estimated by a subjective appraisal of all available evidence. Such evidence suggests that the densities in the lowland areas to the west are, in general, similar to those on the more intensively studied survey plots in the northeast sector.

If we accept the rough figures and estimates presented above, the total population of Mountain Gorillas probably lies somewhere between 3,000 and 15,000 individuals.

## Ecological Distribution

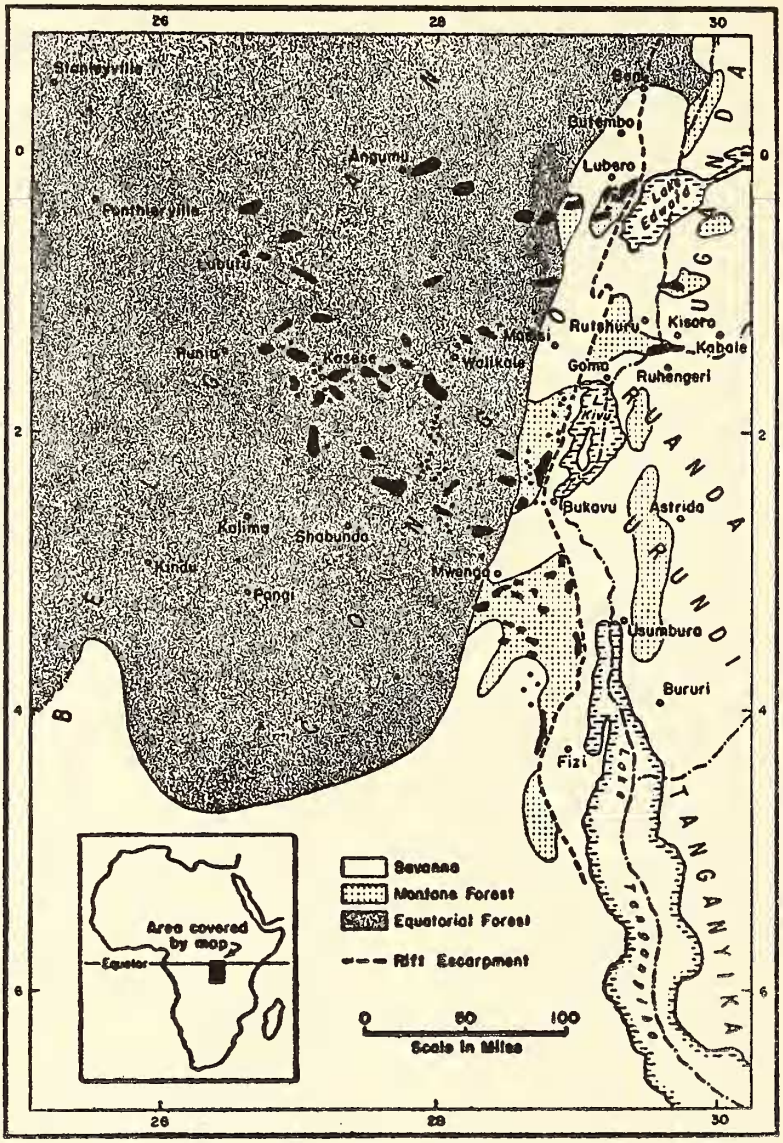
Although the range of the Mountain Gorilla is small, it possesses considerable ecological diversity. Gorillas are found at altitudes ranging from 1,600 feet on the Lowa River above Kima to over 13,000 feet near the summit of Mt. Muhavura in the Birunga Volcanoes. Frosts occur frequently on the higher slopes of the volcanoes while temperatures are decidedly tropical in the areas west and south of Walikale. The topography is notably rugged along the eastern front from Lubero to Fizi but becomes quite flat in many parts of the western region. Gorillas seemed to favor steep slopes and were characteristically associated with the hillier sections where there was a choice. In the precipitous mountains of the Rift gorillas often frequented slopes very difficult for us to negotiate in following them.

Vegetation is of major importance in gorilla distribution. The animal's range lies wholly within the forest zone though extending to its very edge as it borders on the grasslands or plains to the east and the savannah-woodlands to the south. Keay (1959) recognizes two major forest types in this area, the boundaries of which are shown, together with the gorilla distribution data, in Text-fig. 3. Of the 60 gorilla concentration areas plotted on this map, 25 are located in forests classified by Keay as belonging to the Montane Forest Communities, and 35 in the Equatorial Forest or "Evergreen Forest of Low and Middle Altitudes." There are no obvious indications of preference for one or the other of these two types in our data except in the southern region where range extension is greatest in the Montane Forest zone.

### I. *Montane Forest Communities*

Montane Forests can be divided into a number of subtypes with irregular and interdigitating distributions (Keay, *op. cit.;* Lebrun, 1935; Robyns, 1948), four of which are utilized extensively by gorillas. Each of these, in turn, has distinctive seral stages of regeneration. The pertinent sub-types of the "Montane Forest Communities" are listed and described below together with comments on their utilization by gorillas:

(a) *Bamboo Forests.*—Pure stands of bamboo such as those found in the Volcanoes are characterized by a dense though shallow and rather translucent canopy 20 to 25 feet above the ground, roofing an essentially open subcanopy and supported by an abundance of irregularly clustered subvertical stems. The shrub and ground strata are sparse and low or completely absent (Text-fig. 4a). Bamboo forest is a prominent type at altitudes of 7,000 to 9,000 ft. in the Lubero and Birunga Volcano regions and locally elsewhere, forming pure stands or mixtures with various low broad-leafed trees. It supplies food and shelter for gorillas but is util-

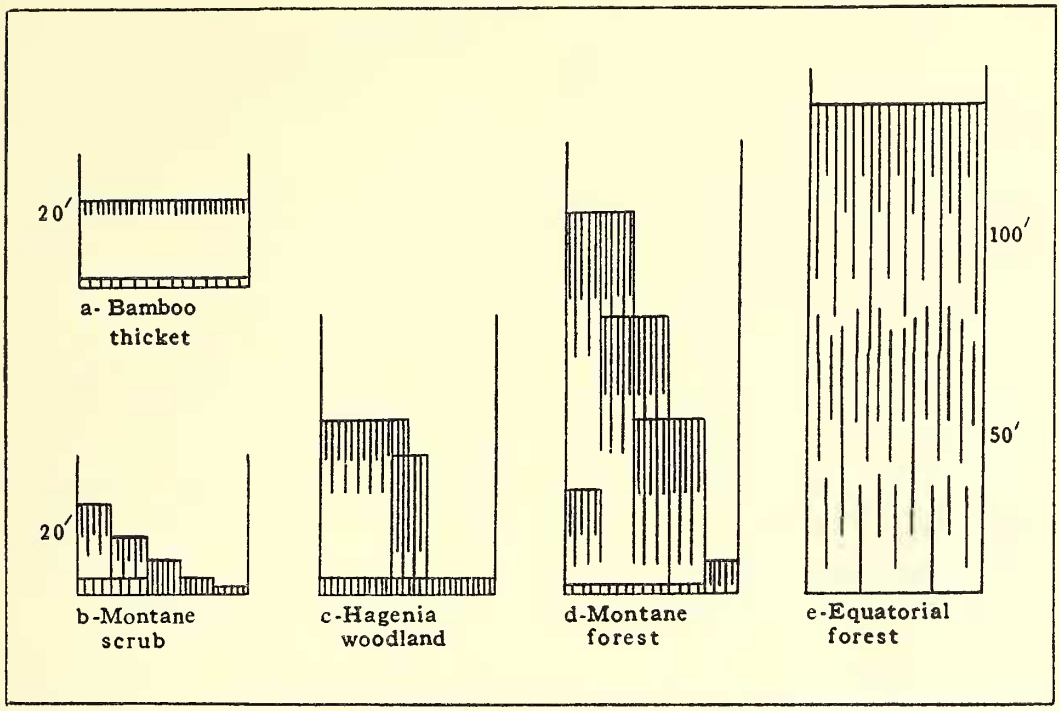



TEXT-FIG. 3. Distribution of the Mountain Gorilla with respect to vegetation types. The indicated boundaries of the Equatorial Forest and the "Montane Forest Communities" are taken in substance from the new UNESCO map (Keay, 1959), refined in some details on the basis of large-scale local maps and personal observation.

ized extensively only in mixed stands and along borders.

(b) *Montane Scrub Forest.*—The low forest above the bamboo zone in the eastern part of the Volcanoes is a mosaic of rather dense 20-, 15- and 10-foot leafy canopies interspersed with open patches of three-foot sedges and herbs (Text-fig. 4b). Scrub forests of this general physiognomy are found irregularly distributed at altitudes of about 10,000 feet along the Rift ridge and on the Birunga Volcanoes. Gorillas occur sporadically in these forests wherever tall herbs are prominent in the understory.

(c) *Hagenia Woodland.*—In its best form in the central part of the Birunga Volcanoes, this type presents a rather dense but incomplete canopy 40 to 50 feet in height supported by heavy, sub-horizontal, epiphyte-covered branches. The subcanopy is quite open, especially under pure stands. Sufficient light penetrates to suport a




TEXT-FIG. 4. Schematic diagrams depicting the height, cover and stratification characteristics of the five principal vegetation types utilized by Mountain Gorillas. Heights are in feet; foliage density is indicated by intensity of shading. In general, the best gorilla habitats are those which have the rankest herb stratum. The diagrams depict conditions in mature stands. For verbal description and gorilla utilization see text.

luxurious and almost continuous stratum of herbs about five feet tall (Text-fig. 4c). This type is largely confined to the Birunga Volcanoes, but the two dominant tree species also occur in mixtures with other Montane evergreens to produce stands intermediate between this and type *d*. It is excellent gorilla habitat.

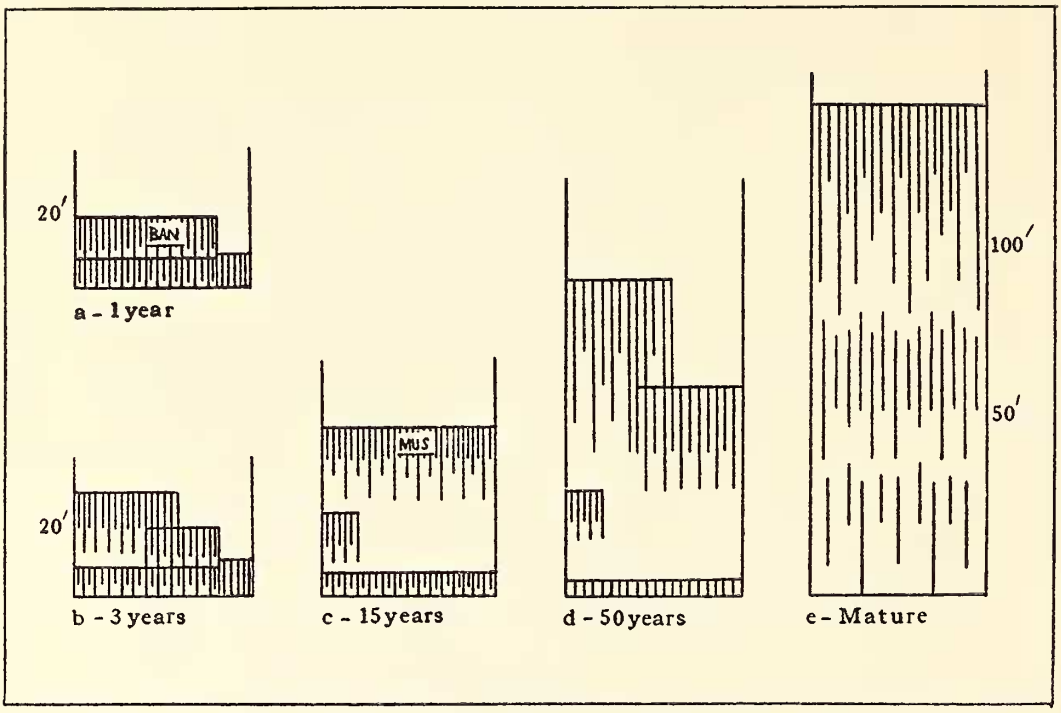
(d) *Montane Evergreen Forest.*—Apparently mature stands of this type along the ridge of the Rift Escarpment as at Mulenge have an incomplete upper canopy 80 to 120 feet high and several indistinctly defined lower canopies. Epiphytes are quite numerous. The herb-shrub stratum is sparse and low where the tree canopy is continuous but quite dense under breaks in the canopy (Text-fig. 4d). This type seems to be best represented in the Mwenga-Fizi region but is also found in the Kahuzi, Lubero and Kayonza Forest areas.[2] It tends to be quite irregular on rough topography with highest canopies on the gentler slopes and a low, more continuous canopy on the ridges. It is rather inferior as gorilla habitat except along edges and where regenerating.

The three gorilla troops whose activities and movements we followed in the Birunga Volcano area all wandered back and forth between several forest subtypes. Because of the patchy nature of forest distribution in these areas it seems unlikely that any gorilla troops are confined to a single type. In the less varied forests of the Rift rim and the Kayonza forest, however, many animals must live entirely within the Montane Evergreen Forest type, its seral stages and the bordering areas of elephant grass, bracken and tree fern.

II. *Equatorial Forest*

Mature equatorial forests are said to be quite uniform in physiognomy throughout their broad range west of the Rift Escarpment. Very little mature forest remains, however, and the various seral stages of regeneration form an intricate and irregular mosaic throughout the region. Selected stages in this regeneration process are described below with comments on their utilization by gorillas. The diagrams in Text-fig. 5 are merely subjective evaluations of conditions and are not based on specific data.

[2]These tall forests are at times transitional with equatorial forests and some have been classified as such. At higher altitudes they are shorter and with more epiphytes and fewer lianas.




TEXT-FIG. 5. Schematic diagrams depicting the physiognomic characteristics of five seral stages in the recovery of equatorial forest following a clearing for banana cultivation. Times given are very approximate.

*Newly Cleared Field.*—Equatorial forests are characteristically cleared for cultivation in a crude and incomplete manner with simple hand tools and fire. A field is generally irregular in shape and a few acres in extent, with a scattering of hardwood trees and "Spirit" trees left uncut. Stumps six to eight feet high are left standing, and the ground remains strewn with half-burned fallen logs. Plantings of manioc or rice and bananas are made almost immediately in shallowly turned soil. Gorillas are often seen at the edges of newly cleared fields and may briefly wander into them.

(a) *At One Year.*—Banana plants reach their full height of about 20 feet in a year and are harvested at about that time. They form a rather dense but irregularly broken canopy down to the ten-foot level. Herbs and vines form a substratum from this point to the ground (Text-fig. 5a). Gorillas visit such stands for food (banana stems and various other herbs) but retire to bigger timber for resting and sleeping.

(b) *At Three Years.*—After a few years the bananas which remain and the new ones which have sprung from the rootstocks of the originals are gradually choked out by second growth trees, vines and shrubs. The whole makes a dense tangled mass, but a partially open subcanopy is usually present under the taller trees (Text-fig. 5b). This is excellent gorilla feeding habitat.

(c) *At Fifteen Years.*—The second growth Musanga trees are now 40 to 50 feet tall and produce a rather thin canopy of big leaves over an open subcanopy.[3] Young specimens of more durable species of trees form an incomplete second story of 10 to 20 per cent. The herb stratum is luxurious and about five to six feet tall (Text-fig. 5c). Gorilla utilization is now declining, but much food remains and the dominant Musangas provide both food and favored bedding situations.

(d) *At Fifty Years.* In many parts of the Kivu Province, the demands for agricultural land force a recutting of regenerating forests every 10 or 20 years. In more inaccessible areas away from settlements and roads, however, older forests are found which show signs of immaturity presumably related to land clearing activities in early times. These forests may have upper canopies 100 or more feet high, but incomplete and uneven. There is also a large num-

[3]According to Ross (1954), the life span of this tree is about 15 to 20 years.

ber of younger trees pushing up through the subcanopy, and, importantly, a definite lower stratum of herbs and ferns (Text-fig. 5d). Gorillas find considerable food in this herb stratum.

(e) *Mature Equatorial Forest.* — A mature equatorial forest in the central Kivu Province has a nearly complete canopy 120 to 180 feet high and a rather even, thinly foliaged subcanopy, sometimes vaguely divisible into several strata, extending down to the ground. Herbaceous and ground vegetation is very sparse or absent (Text-fig. 5e). The mature forest, presumably because of the scarcity of food materials near the ground level, is sparsely inhabited by gorillas.

Gorilla distribution in the equatorial forest region is determined to a considerable extent by the amount and distribution of patches of regenerating forest. The optimum situation is provided by a mosaic of old fields in various stages of regeneration.

## Distributional Dynamics

An examination of the maps in Text-figs. 1 & 3 shows that many of the larger population units are located flush against prominent physical barriers such as rivers, escarpments and forest boundaries. The Lugulu River north of Shabunda, the Luka and Lowa Rivers west of Walikale and the eastern forest boundary from Fizi to Lubero are examples. The impression suggested by this situation is that there has been a centrifugal expansion from one or more centers, a piling up of animals against certain major barriers, and perhaps a partial evacuation of large tracts near the centers.

*Range Boundaries.*—The factors limiting dispersal at the north, east, south and west boundaries each present special problems. A problem of the northern region is the bridging or circumventing of the Oso-Lowa River barrier. We incline to the theory that the region above this barrier was invaded from the south, but regardless of the direction of movement the problem of a crossing remains to be explained. The gorilla is notoriously shy of water[4] and a direct fording or rafting of this formidable river system west of the vicinity of Masisi is unlikely under conditions resembling those which prevail today. Either the penetration was made during an ancient interpluvial period of low water or was accomplished near the headwaters. This second possibility presents other difficulties associated with the crossing of expanses of what is now open grassland, but is supported by the presence of isolated colonies on forested "islands" in the Rift valley floor. It suggests passage during a pluvial period with expanded forest boundaries.

The eastern boundary of the range is nicely demarcated by the Rift Escarpment along much of its length (Text-fig. 3). The absence of gorillas in the broad tongues of montane grassland which extend up over the rim north and south of Lake Kivu, however, indicate that the actual effective barrier is not the escarpment itself, but the forest-grassland boundary. As already noted, two populations have penetrated this barrier and established themselves on montane-forest "islands" in the predominantly grass-covered valley floor. The crossing to the eastern volcano area was probably by way of irregular forest bridges on Mts. Nyamuragira and Nyiragongo, presumably in pluvial times. The population in the Kayonza Forest to the north probably arrived there by way of the volcanoes. The Semliki Plains apparently have constituted an effective barrier to dispersal into the Ruwenzori forests east of Lubero.

The southward extension of gorillas into the Mwenga-Fizi region probably occurred near the headwaters of the Lugulu and Ulindi Rivers. It is interesting and perhaps significant that this southernmost arm of gorilla range lies entirely within the montane forest zone. The fragmented nature of the populations in this region and the small size of the units may be related to the highly irregular topography and vegetation.

We have no explanations or worthy speculations on the limiting factors of the western boundary from the Lugulu River to the Maiko. Altitudes become progressively lower, prevailing temperatures higher and agricultural operations more intensive, but none of these conditions seem adequate to explain the abrupt discontinuation of gorilla populations short of the Lualaba River.

The occurrence of a separate population of gorillas (*G. g. gorilla*) in the Cameroons and Gabon 1,000 miles to the west is evidence for a former occupation of the intervening regions. Vague and inconclusive records suggest that gorillas may have occurred north of the great bend of the Congo within the past few hundred years (Coolidge, 1936), and physiographic features argue strongly that the connection which provided the assumed channel for gene exchange must have been located in this region and around the headwaters of the various large rivers of the right bank. This region now supports a savannah vegetation unsuitable for gorilla habitation, and we conclude that the bridging populations must have lived here during one of the pluvial periods

[4] In driving animals into capture nets C. Cordier could not force gorillas to cross streams more than 15 or 20 feet wide and two or three feet deep.

of the Pleistocene when the forest boundary lay farther north than at present.

*Local Distribution.*—As already noted, gorillas are not randomly distributed through the forest but are aggregated for the most part into small, well-defined population units on concentration areas comprising only about 5½ per cent. of the total range. In some cases the boundaries of these areas coincide with natural boundaries which appear to have operated as barriers to dispersal, but in most cases the forest continues unchanged, and we have been unable to find a simple explanation for the discontinuity.

Social behavior acts as an aggregating factor at least at the local level. Gorillas tend to live in troops of about 5 to 20 individuals and to restrict their activities for extended periods to home ranges of familiar terrain (unpubl. data). From a few to several dozen such troops combine to make a population unit, apparently selecting contiguous home ranges rather than dispersing themselves randomly through the forest. The nature of these social interactions and their role in the derivation of clumped distribution patterns is now being investigated.

The actual geographic pattern of distribution of concentration areas is undoubtedly determined by a combination of physical and environmental factors operating through time. Population units probably drift or are pushed about as local conditions change. Evidence for movements of this sort was encountered in a number of reports of recent invasions and of evacuations or extirpations. More often, however, our informants told of local stability over periods of several decades. Written records, furthermore, suggest a general stability of distribution in the Lubero and Birunga Volcano areas for 30 to 40 years.

As noted above, physical barriers have apparently influenced and in part determined the present location of many of the concentration areas. Of the 60 areas plotted on our map, 17 have one side bordering on a large river, and 13 front on the forest-grassland boundary. Without historical data we can only guess as to how this situation developed, but one is tempted to visualize the population units slowly drifting over the map like wandering amoebas until their progress is physically blocked by a barrier. In those cases where man has moved the location of a barrier as by pushing back the forest boundary, the retraction of the population unit has been as immediate as it was inevitable.

The forces or influences responsible for the drifting of population unts within the outer boundaries set by physical barriers can be visualized, at least in part, by examining the effects of man-made disturbances at the local level. The most important of these disturbances during the last century has been the repetitive clearing of the forest in small patches to create a shifting kaleidoscopic pattern of successional stages of forest regeneration. Gorillas have responded by adjusting their local foraging activities to meet the temporarily favorable conditions created in the recently cultivated fields. There is also evidence of the expansion or movement of gorilla population units into developing agricultural or mining regions. The large concentrations of gorilla areas around Kasese and south of Mwenga correlate with a heavy influx of native families into these mining areas in recent times. A road engineer east of Kasese found gorillas moving in around the workers' villages and garden plots while construction work was still in progress, and several mining engineers told of gorillas appearing around new camp sites within a year or two of their establishment. Such incompletely documented anecdotes may represent returns after initial displacement rather than actual invasions, but in either event they suggest a certain fluidity of movement.

The long-standing government policy of resettling natives from the deep forests on relatively narrow strips along the roadways probably accounts in part for the present concentration of gorillas along these human thoroughfares and their relative scarcity in the hinterlands. The animals have apparently moved into these disturbance areas and remained despite persistent harassment. A long-established mining community surrounded by the villages and shambas of native workers may thus form a sort of nucleus for a gorilla population unit as at Utu, Kima or Lulingo.

Further evidence for the role of rotational forest clearing in gorilla movements is found in historical records of evacuation by gorillas following the emigration of human populations. The first consequence of an exodus of human beings may be an improved environment freed of direct human disturbance. Thus the village of Mangombe near Kima still had a large local population of gorillas three years after it was abandoned as a mining camp and allowed to grow up to a jungle of shrubs and vines. A former resident reported that "the gorillas from the surrounding shambas moved into the village as the people moved out." Abandoned mining centers like those near Lutunguru and Alimbongo apparently had good gorilla populations during and immediately following their period of activity and have subsequently lost them. It must be said, however, that the records here are

very fragmentary and quite controversial.

The old and long-abandoned Arab slave route[5] from Angumu to Walikale resulted in vegetational disturbances which can still be detected by foresters and which apparently drew gorillas in from the surrounding deep forests. Reports reaching government surveyors told of gorillas persisting in this area for many decades, but current reports indicate that the animals have now largely disappeared.

As with most studies of distributional dynamics, our direct observations are limited to the effects of man-made disturbances operating over a very limited period of time. Our documentation of the environmental disturbances and distributional responses of prehistory are much less precise, but the evidence for frequent and major disturbances is overwhelming, and we can assume that responses in the past were basically similar to those we observe today. Gorilla distribution has thus been a dynamic phenomenon from time immemorial and doubtless will continue to be.

What the observed tendencies and trends indicate for the fututre of the Mountain Gorilla varies in different parts of the range. Peripherally and in the areas of good arable soils as in the Volcanoes, the Kayonza Forest and the Lubero district, range boundaries are rapidly being pushed back by the conversion of land to stabilized agriculture. The continued existence of gorillas in these regions will depend on the maintenance of reserves set aside for the preservation of gorilla habitat, *i.e.* large continuous expanses of suitable forest. The rigid protection against all types of human disturbance in the Albert Park gorilla sanctuary has been extremely desirable from many points of view, but experience in other areas indicates that complete control of trespass is not always necessary. Excessive disturbance must be avoided, but above all, the destruction of habitat by forest clearing must be stopped.

In the equatorial forest zone west of the Rift Escarpment the conditions and needs are totally different. Here the boundaries of the gorilla range are little affected by pressures of land utilization except around the large population centers. Conditions of soil and climate enforce and will probably continue to enforce a type of agriculture which is beneficial rather than destructive to gorilla habitat. Protection of the forest against this rotational system of agriculture would actually be undesirable. Gorilla conservation here must take the form of restrictions on killing. Present killing rates are apparently not serious, but the introduction of even small numbers of firearms would be disastrous regardless of legal restrictions on their use.

Above all it must be remembered that the total geographic range of the Mountain Gorilla is extremely small, and the history has shown that animals so situated are highly vulnerable.

[5]This route led south of Lake Kivu into Tanganyika and was probably at its peak of activity during the 1880's.

## Summary

The total geographic range of the Mountain Gorilla in 1959 covered an area of about 35,000 square miles south of the equator and west of the Albertine Rift. Within this range the animals were mostly aggregated into about 60 small areas of concentration covering roughly 1,900 square miles of forest habitat. Population densities within these areas probably ran between one and five animals per square mile.

Gorilla populations were found through several climatic zones and in various types of forest. They were most numerous where there was an abundance of herbaceous undergrowth as in fairly open stands or in patches of secondary forests in early stages of regeneration.

The location of concentration areas along rivers and forest edges suggests that population units, though relatively stable and localized over periods of decades, may drift within boundaries prescribed by physical barriers. Evidence for such drifting is provided by observations on distributional responses of populations to man-made changes in the forest habitat.

The future of the Mountain Gorilla depends on the protection of tracts of forest habitat in the eastern areas and on the control of firearms in the equatorial forest areas west of the Rift.

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## Literature Cited

Coolidge, H. J.

1929. A revision of the genus Gorilla. Mem. Mus. Comp. Zool., 50: 291-381.

1936. Zoological results of the George Vanderbilt African expedition of 1934. Part IV. Notes on four Gorillas from the Sanga River region. Proc. Acad. Nat. Sci. Phila., 88: 479-501.

Keay, R. W. J.

1959. Vegetation map of Africa south of the Tropic of Cancer. Oxford Univ. Press, London, 24 pp.

Lebrun, J.

1935. Les essences forestières des regions montagneuses du Congo oriental. Publ. Inst. Agron. Congo Belge, Ser. Sci. 1.

Robyns, W.

1948. Les territoires phytogeographiques du Congo Belge et du Ruanda Urundi (Inst. Roy. Col. Belge, fasc. 1).

Ross, R.

1954. Ecological studies on the rain forest of Southern Nigeria. III. Secondary succession in the Shasha Forest Reserve. J. Ecol., 42: 259-282.